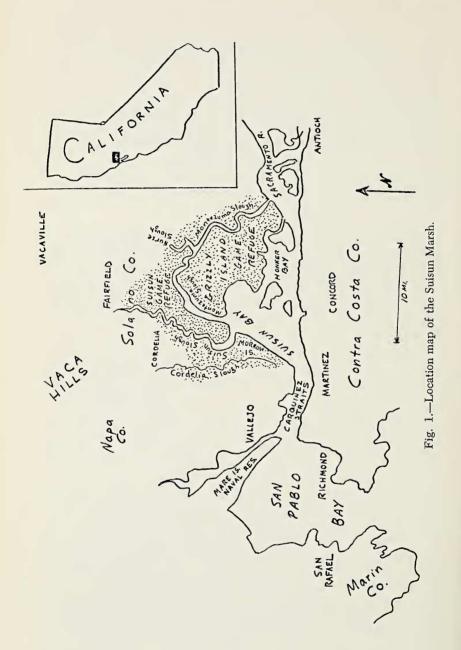
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BUTTERFLIES OF THE SUISUN MARSH, CALIFORNIA ABTHUR M. SHAPIRO

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At the time of European colonization, California had an estimated five million acres of wetlands. By 1973 only a tenth of that acreage remained, with a current rate of loss of one percent per year. California, unlike the eastern United States, is considered to have a depauperate marsh fauna of butterflies, and its wetlands have received very little attention from collectors.

The Suisun Marsh is a complex of tidally influenced wetland habitats covering some 44,000 acres in Solano County, westcentral California, and is one of the largest marsh tracts remaining in a reasonably natural state on the entire Pacific coast. The Marsh occupies a structural basin hemmed in by hills on three sides. These hills, part of the Coast Ranges, are arid in summer and are covered with annual grassland or open oak woodland. They apparently confer sufficient isolation on the Marsh to produce several endemic taxa of plants and animals; among these the most prominent are the Suisun Shrew (Sorex sinuosus) and the showy Composites Grindelia paludosa, Cirsium hydrophilum, and Aster chilensis ssp. lentus. As may be seen from Figure 1, the Marsh communicates with San Francisco-San Pablo Bays to the west and the Sacramento-San Joaquin Delta to the east, and through the latter with the Central Valley of California. A biotic connection with the San Francisco Bay salt marshes is shown by the ranges of two endemic species shared by them, the Salt-Marsh Harvest Mouse (Reithrodontomys raviventris) and the Composite Grindelia humilis.



CLIMATE OF THE MARSH

The Suisun Marsh differs from the Central Valley in being exposed to a stronger maritime climatic influence, which enters the basin by the Carquinez Straits. At the same time the climate of the Marsh is more continental than those of the valleys which open directly to the coast. Aside from moderating both summer and winter temperature extremes, the maritime effect increases the frequency of morning fog and low cloudiness as compared to the Central Valley, e.g. Vacaville ten miles to the east; but unlike immediate coastal sections, the Marsh very rarely has persistent fog or cloud in summer. More dramatically, the maritime air produces frequent sustained high winds as it rushes through the Straits to fill up the thermal low-pressure trough in the interior. Winds in excess of 20 knots probably occur on 100 days or more each year in the Marsh, blowing usually from the west ("Suisun" means "west wind" in the local Indian dialect, and is still used locally as a name for this wind).

The U.S. Weather Bureau maintains a reporting station at Fairfield. This location receives from 30-50 days with maximum temperatures greater than or equal to 90°F (32.2°C) and 15-40 days with minimum less than or equal to 32°F (0°C) per season. Temperatures in excess of 100°F (37.7°C) occur 3-5 times/season and below 30°F (-1.1°C) a similar number of times. Data for 1971 and 1972 monthly temperatures are given in Table 1. Precipitation of about 24 inches falls from October to May; there is little or no precipitation in summer. Relative humidity in summer is, however, consistently higher than in the Sacramento Valley and the Marsh is sheltered from the full force of the hot, dry "northers" which produce the most extreme summer weather in the Valley.

HABITATS OF THE MARSH

Most of the Suisun Marsh is under the control of hunt clubs whose management practices vary widely. Portions of the Marsh are cut over or burned from time to time; through an extensive system of levees, ditches, and gates the water level may be manipulated on individual parcels of land. Soil salinity is thus extremely variable from parcel to parcel. The overall result is a complex vegetational mosaic which for convenience may be divided into "high marsh," "low marsh," and "landfill."

Temperature data in °F for Fairfield Fire Station, California, 1971-72. Table 1.

	Fr.													
	days <32°F	18	т	0	0	0	0	0	0	0	0	ref	13	35
1972*	days >90°F	0	0	0	0	4	œ	σ	12	Н	0	0	0	: 34
	extremes lowest	24	31	34	37	43	77	51	67	94	38	32	19	Totals:
	Monthly extremes highest lowest	56	71	82	80	95	103	108	66	06	88	89	89	
	min.	32.7	41.0	44.5	4.44	48.5	52.1	56.3	56.7	53.8	51.3	42.8	34.5	
	Mean T, °F max. min	9.67	6.09	70.4	69.2	79.1	85.1	84.6	87.7	82.0	71.7	59.6	6.67	
	days <32°F	7	2	e,	0	0	0	0	0	0	0	0	11	23
	days >90°F	0	0	0	0	0	5	11	17	15	2	0	0	Totals: 50
1971	Monthly extremes ighest lowest	26	31	29	38	36	43	20	51	43	37	33	27	Tota
	Monthl highest	65	70	77	79	82	97	66	106	107	91	76	63	
	min.	38.0	38.1	42.8	43.7	48.2	53.1	55.5	57.4	54.0	45.0	40.2	34.9	
	Mean T, °F max. min	55.0	60.5	64.4	68.1	72.0	82.2	88.2	90.2	87.4	75.5	0.49	51.9	
	Month	ы	ĺΣι	×	A	×	ט	'n	A	ιo	0	Z	Д	

*Although 1972 was a "cool" year, a brief period of record-breaking heat occurred in July.

"High Marsh" — This group of associations occurs in areas of low salinity: high points (islands) within the Marsh, levees and the edges of sloughs, ditched marshland and fresh-water pools. It has the highest plant species diversity in the Marsh, and is characterized by the aspect dominance of showy Composites in late summer. Some characteristic plant species are: Grindelia humilis, G. paludosa, Aster chilensis ssp. lentus, Baccharis douglasii, Cirsium hydrophilum, Solidago occidentalis, Achillea borealis ssp. arenicola, Pluchea purpurascens, Cicuta bolanderi, Apium graveolens, Potentilla egedei, Atriplex patula var. hastata, Phragmites communis var. berlandieri, Scirpus olneyi, S. koilolepis, S. acutus, Juncus effusus var. brunneus, and Typha latifolia.

"Low Marsh" — This association, or group of associations, covers the most extensive part of the Marsh. It occupies areas of high salinity which are saturated or shallowly inundated at high tide. The dominant plants throughout are Distichlis spicata and Salicornia virginica. Characteristic associates are: Atriplex patula var. hastata, Lilaeopsis occidentalis, Polygonum aviculare var. littorale, P. fowleri, Cotula coronopifolia, Frankenia grandifolia, Eryngium articulatum, Rumex crispus, Juncus acutus

var. sphaerocarpus, J. bufonius, and Scirpus olneui.

"Landfill" — In many places marshland has been filled in with construction debris or other refuse, or with clay soils from the uplands. Plants found in such sites are typical weeds of highly disturbed lowland sites in California: Centaurea solstitialis, Cichorium intybus, Lactuca serriola, Cirsium lanceolatum, Silybum marianum, Malva rotundifolia, M. nicaeensis, Sida hederacea, Convolvulus arvensis, Epilobium paniculatum, Atriplex rosea, A. semibaccata, Polygonum aviculare, Foeniculum vulgare, Bromus rubens, B. rigidus, Avena barbata, etc. The transition from marsh to annual weeds occurs at about four feet above sea level, the mean highwater mark at Suisun. Baccharis pilularis ssp. consanguinea and Tamarix pentandra form thickets just above this level.

THE BUTTERFLY FAUNA

So far as I have been able to determine, the Suisun Marsh has never been collected systematically for butterflies before 1972. In 1972 and 1973 I visited it at frequent (usually 2-4 weeks) intervals and recorded all butterfly species present. The seasonal distributions of the 40 species recorded are given in Figures 2 and 3. It is likely that one more resident and five to

ten immigrant or stray species (from the hills) may be found in the Marsh. All of the resident species recorded in the Marsh occur in both the San Francisco Bay area and the Central Valley (except Ochlodes yuma, unrecorded from the Bay but to be expected). Two endemic populations of widespread species occur in the Suisun Marsh. They are the Potentilla-feeding strain of Lycaena helloides and the large, richly colored Phyciodes campestris associated with Aster chilensis ssp. lentus. Both have been sought, but not yet found, in salt marshes around the Bay area and in Marin County. They are discussed individually, below.

SYSTEMATIC LIST

Danaus plexippus (L.) — Occasional to frequent, especially in autumn; throughout. Larvae on Asclepias fascicularis on land-fill. Does not overwinter at Suisun.

Coenonympha tullia california West. — Rare stray from the hills; not known to breed in the Marsh. Is is striking that the *C. tullia* complex has not evolved salt-marsh populations on the Pacific Coast as it has elsewhere in its vast range.

Speyeria coronis (Behr). — One female, certainly a stray from the hills. No violets are recorded in the Marsh, but Viola pedunculata occurs in the Potrero Hills and on Mt. Diablo.

Euphydryas chalcedona (Dbldy). — One male, a stray from the hills.

Phyciodes mylitta (Edw.).—Frequent on levees and high marsh; multiple-brooded. Larvae common on Silybum on landfill, but not yet found on Cirsium hydrophilum.

Phyciodes campestris (Behr). — Unaccountably rare. The 7 Marsh specimens are phenotypically very distinct from the usual lowland P. campestris (Fig. 4), particularly in the lack of contrast between the median spot-band and the ground color; the very well-developed submarginal spot-band; the reduced amount of black above; and the larger size. They were taken on flowers of Aster chilensis ssp. lentus and may represent an endemic population developed in association with this plant, but until more information and specimens become available it seems best to defer naming them.

D. plexippus	vi.25	vii.16	vii.23	viii.25	ix.23	x.21	xi.5
C. t. california			X	X	X	X	
S. coronis							
E. chalcedona					Х		
P. mylitta							
P. campestris		X	Х		Х		
N. antiopa	v						
N. californica	X						
V. atalanta							
C. virginiensis						Х	
C. carye	х	х	х	х	х	X	Х
C. cardui	Λ.	Λ.	Λ	Λ	X	Λ	Λ
P. coenia	х	Х	х	Х	X	Х	Х
L. lorquini	A	Α	Α	21.	A	Α	11
L. bredowii							
S. melinus	Х	х	х	X	Х	x	
S. sylvinus		**	••	••			
S. californica							
L. helloides	х	х	х	х	x	х	х
L. xanthoides	X	X	••	••	••	••	••
B. exilis	X	x	Х	X	х	х	х
	X		x	••			- T
E. comyntas	X	х	X	X	Х		
P. acmon							
E. ausonides	Х	Х	х	Х	х	X	х
C. eurytheme	X	X	X	Х	X	X	
P. rapae							
P. protodice							
B. philenor		17		v	х	х	X
P. zelicaon		Х		Х	Х	Х	Х
P. rutulus				v			
E. tristis	х	х	х	X X	х	Х	Х
P. communis	Λ	X		X	X	Λ	Λ
P. scriptura	х	X	X X	X	X	Х	х
P. catullus	X	X	X	X	Λ	Λ	X
H. phylaeus	Λ	X	X	Λ			^
A. campestris	х	X	X	Х	х	х	х
P. sabuleti	Λ	Λ	X	X	X	Λ	Λ
0. sylvanoides	х		X	Λ	Λ		
Q. yuma	Λ	х	21	Х	х	Х	Х
L. eufala							
Total species:	16	18	19	18	19	14	11

Fig. 2.—Seasonal distribution of butterflies at Suisun, 1972.

Fig. 3.—Seasonal distribution of butterflies at Suisun, 1973.

xii.3	×										*	×								
xi.26	×										×									
xi.18 xi.26											×	×	×							
x.26	×				×	×			×	×	×	×	×		×	×			×	
x.20 x.26	×				×	×			×		×		×			×			×	
x.12	×				×	×	×	×	×		×	×	×	×		×			×	
ix.21	×									×	.⋈	×	×			×			×	
111.13	×										×	×	×			×			×	
.22 vi	×	×			×						×	×	×			×			×	
v.28 vi.6 vi.30 vii.8 vii.22 viii.13	×										×	×	×			×			×	×
1.30 v	×	×			×				×	×	×	×	×	×		×			×	×
i.6 vi					×		×				×	×	×			×	×		×	×
.28 v				×	×		×				×	×	×			×	×	×	×	×
19 v																×				
.6 v.											×	*	25			*			×	25,
iii.18 iv.8 v.6 v.19									×		×	×							~	
18 1																				
111.		m									×	×								
n levinnie	enddive	C. t. california	conis	E. chalcedona	litta	P. campestris	lopa	N. californica	V. atalanta	C. virginiensis	ye	inpi	enia	L. lorquini	L. bredowii	linus	S. sylvinus	S. californica	L. helloides	L. xanthoides
010		; t.	S. coronis	3. che	P. mylitta	can,	N. antiopa	l. cal	7. ata	L vin	C. carye	C. cardui	P. coenta	101	. bre	S. melinus	3. syl	3. cal	he	Xar
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× ×	* * *		* * *	××	16
× ×	× ×	××	× × ×	××	19
× ×	× ×	×	× × ×	× × ×	18
× × ×	* *	×	* * *	×	22
× × ×	× ×	×	× × ×	×	19
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×	××	×	×	××	13
×	××	×	× ×	×	10
××	××	××	××		11
×	××	× ×			7
b. exilisE. comyntasP. acmonE. ausonides	C. eurytheme P. rapae P. protodice B. philenor	P. zelicaon P. rutulus E. tristis	P. communis P. scriptura P. catullus	H. phylaeusA. campestrisP. sabuletiO. sylvanoides	 yuma L. eufala Total species:
க் ங் ஃ ங்	ப்ப்ப்	P1 P1 P1	P4 P4 P4	H A G	9 1 1

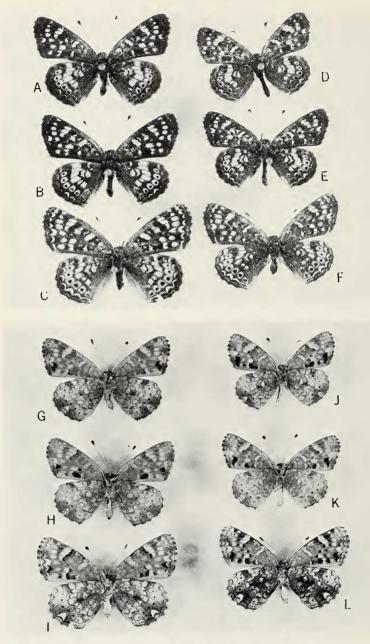


Fig. 4.—Phyciodes campestris from lowland central California. a-c, g-i, Suisun Marsh, X.12.73; d-f, j-l, Willow Slough, Yolo Co., X.19.73.

Nymphalis antiopa (L.) — Occasional throughout. Larvae occasionally abundant on Salix lasiandra along ditches.

Nymphalis californica (Bdv.).—Occasional as a migrant through the Marsh, but not breeding; no Ceanothus occur in the basin. Vanessa atalanta (L.). — Occasional throughout, mostly in high marsh; multiple-brooded. Larvae on Urtica holosericea (Joice Island).

Cynthia virginiensis (Drury). — Occasional throughout; the least common Cynthia, but still commoner than in most of the Sacramento Valley. Larvae on Gnaphalium bicolor (Joice Island; levees near Suisun City).

Cynthia carye Hbn. (= annabella Field).—Common everywhere; multiple-brooded. Larvae common on Malva rotundifolia, M. nicaeensis, Althaea rosea, and Sida hederacea (all Malvaceae) on landfill. A striking aberration was taken in the Marsh, v.19.73, figured in Shapiro, 1973.

Cynthia cardui (L.). — Common throughout. Does not appear to overwinter. Larvae on Silybum marianum, Cirsium lanceolatum, Centaurea solstitialis, Malva spp., and Amsinckia douglasiana on landfill; on Cirsium hydrophilum on high marsh.

Precis coenia (Hbn.). — Common to abundant everywhere, especially in late summer and autumn; September-October specimens are often very red beneath. Larvae on Plantago coronopus in low marsh, P. lanceolata and Lippia nodiflora on landfill.

Limenitis lorquini (Bdv.). — Occasional along sloughs near willows, probably breeding.

Limenitis bredowii californica (Butl.). — Recorded once; stray from foothills.

Strymon melinus Hbn. — Frequent to common throughout, all season.

Satyrium sylvinus (Bdv.). — Locally frequent in clumps of Salix hindsiana along ditches, otherwise not seen.

Satyrium californica (Edw.). — One male, in high marsh on celery blossoms, certainly a stray from the hills.

Lycaena helloides (Bdv.). — Abundant. On landfill associated with *Polygonum aviculare* and *Rumex crispus*; in high marsh, especially deep in the Marsh, with *Potentilla egedei*. The two strains are slightly differentiated phenotypically in a statistical sense, and are not altogether synchronized in brood sequence. See Shapiro, 1974 for a fuller discussion. A bilateral gynandro-

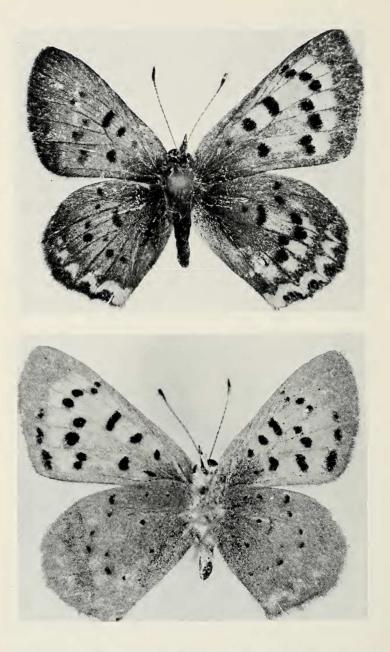


Fig. 5.—Bilateral gynandromorph of Lycaena helloides, Suisun, X.12.73.

morph of the *Potentilla* strain taken in high marsh, X.12.73 is shown in Figure 5.

Lycaena xanthoides (Bdv.). — Abundant on landfill and low marsh, associated with Rumex crispus; one brood. Suisun specimens average smaller and duller in color than Central Valley ones, and show some local differentiation.

Brephidium exilis (Bdv.). — Scarce early in the season, but becoming very abundant in September-October. Throughout, commonest on low marsh and landfill. Larvae abundant on Atriplex patula var. hastata, A. rosea, and A. semibaccata.

Everes comuntas (God.). — Locally frequent along ditches; occasional in high marsh; in spring common on landfill. Larvae on Lotus purshianus, L. strigosus, and Vicia sativa.

Plebeius acmon (West. & Hew.). — Common throughout. Spring and fall males, and spring females of f. vern. "cottlei". Larvae on Polygonum aviculare on landfill.

Euchloe ausonides Lucas. — Frequent to locally common on landfill; occasional on high marsh. Two broods. Larvae on Raphanus sativus and Brassica nigra.

Colias eurytheme Bdv. — Common everywhere, especially in September and October. Larva on Vicia sativa on landfill—doubtless on a wide variety of legumes as elsewhere.

Pieris rapae (L.) — Common throughout. Larvae on Brassica nigra and B. arvensis and Raphanus sativus on landfill.

Pieris protodice Bdv. & LeC. — Occasional on landfill near Suisun City, in annual grassland; strays into marsh.

Battus philenor hirsuta (Skinner). — Occasional stray from nearby canyons; once fresh in Suisun City, xii.3.73.

Larvae abundant on *Foeniculum vulgare* on landfill and levees. *Papilio zelicaon* Lucas. — Abundant on high marsh and landfill. Not recorded on *Cicuta* or *Apium* in high marsh, although both are acceptable in the laboratory.

Papilio rutulus Lucas. — Occasional in high marsh; not known to breed, but suspected of doing so on cottonwoods or willows, as on Joice Island.

Erynnis tristis (Bdv.). — Infrequent on landfill and on high marsh; presumably a stray from the hills.

Pyrgus communis (Grote). — Abundant on landfill; occasional on high marsh; all season. Larvae common on Malva rotundifolia, M. nicaeensis, and (occasionally) Sida hederacea.

Pyrgus scriptura (Bdv.). — Abundant on landfill near the host plant, Sida hederacea.

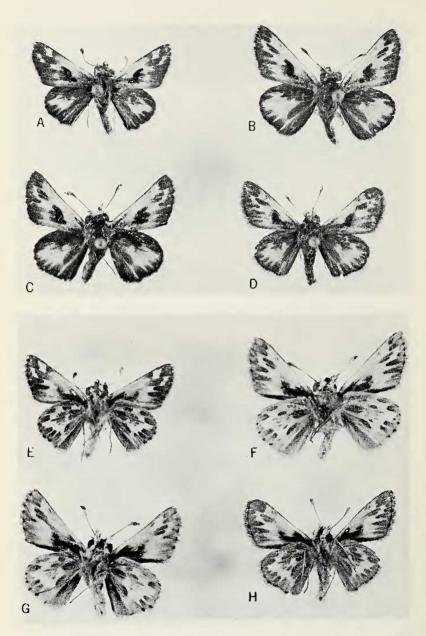


Fig. 6.—Variation in male *Polites sabuleti*. a-c, e-g, Suisun Marsh, X.12.73. d, h, *P. s. tecumseh*, Donner Pass, Placer Co., el. 6975', viii.17.73.

Pholisora catullus (Fabr.). — Common on landfill; occasional on low marsh. Larvae on Amaranthus hybridus on landfill.

Hylephila phylaeus (Drury). — Common throughout, especially in September and October.

Atalopedes campestris (Bdv.). — Frequent on landfill; occasional elsewhere.

Polites sabuleti (Bdv.). — Very abundant on low marsh and landfill. Extremely variable; a few specimens (cf. Fig. 6) indistinguishable from *P. s. tecumseh* of the high Sierras. Larvae common on *Distichlis spicata*.

Ochlodes sylvanoides (Bdv.). — Common throughout; at least two broods.

Ochlodes yuma (Edw.). — Locally frequent around stands of *Phragmites*, as at the Suisun City marina and along Highway 21 north of the Fairfield City Limit. Two broods.

Lerodea eufala (Edw.). — Frequent in all habitats in late summer and autumn. Larvae on Sorghum halepense, Echinochloa crus-galli, and Cynodon dactylon on landfill and along ditches.

DISCUSSION

There is surprisingly little phenological difference in the butterflies of the Suisun Marsh and the Central Valley. The only conspicuous example is *Papilio zelicaon*, which flies into mid-November at Suisun 6-8 weeks after it has disappeared in the Valley. It is also more abundant at Suisun than in the Valley. *Brephidium exilis*, which is largely a species of saline and alkaline situations, is near its northern limit in both areas and may not always overwinter. In 1972 it flew earlier at Suisun than in the Valley, but in 1973 the situation was reversed. Flight activity at Suisun is limited by wind probably to about the same degree as it is prevented by heat and dryness in summer in the Valley. In most of California the maximum numbers of individuals and species fly in spring or early summer; at Suisun this peak occurs in September and October.

The Suisun Marsh receives no summer rain, but its year-round water supply and the halophytic habit of many of its plants provide a constant supply of butterfly host plants and nectar sources. In most of lowland California there is a summer die-off of annuals; most such places have a fauna including many vernal univoltine species. In the nearby Vaca hills in Yolo and Solano Counties 25 of 65 recorded taxa are univoltine (39%), for example. In the Sacramento Valley the moist riparian habitats

and agricultural irrigation allow for a much more multivoltine fauna (8 of 47 breeding taxa are univoltine, 17%). The Suisun Marsh has the most strongly multivoltine fauna recorded in California—only 2 of 33 breeding taxa are univoltine (Satyrium sylvinus, Lycaena xanthoides), or 6%. (Of the 6 immigrant taxa from the hills, however, 3 are univoltine—S. coronis, E. chalcedona, S. californica.) Except for Euchloe ausonides, Lerodea eufala and the two Ochlodes, the remaining species are apparently continuously brooded all season. The brood sequence of Phyciodes campestris is unknown.

Only one additional resident species, *Polygonia satyrus* (Edw.) is likely to be found. Its host, *Urtica holosericea*, is locally common in the Marsh. Almost any common foothill species, and some of the less common ones, may turn up eventually in the Marsh. There is a remote possibility that *Cercyonis pegala ariane* (Bdv.) may turn up somewhere in the Marsh; it is unrecorded in Solano County but is found only 15 miles away in Contra Costa County in similar habitats.

The Suisun butterfly fauna contains a large proportion of weedy or adventive species. This is the case with most of low-land California. Although locally differentiated populations of two species occur at Suisun, the lack of butterflies and skippers associated with the many distinctive plants—especially grasses and sedges—is as striking there as elsewhere. The reclamation of marshland in the Central Valley may have destroyed some endemic Lepidoptera, but the absence of relict populations from places as little disturbed as parts of the Suisun Marsh argues for a genuine lack of wetland species in California.

ACKNOWLEDGMENTS

Several of the records reported here were obtained by Mrs. Adrienne R. Shapiro. Mr. Paul Flores showed us collecting areas on Joice Island. Plants were determined in the U.C. Davis Herbarium.

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